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LOCAL PHOTOSYNTHETIC ECOTYPES IN *PINUS ATTENUATA* AS RELATED TO ALTITUDE

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This paper reports ecotypic variation in *Pinus attenuata* Lemm., as determined by temperature conditioning in greenhouse-grown seedlings from seed collected at the elevational extremes of its range in the San Bernardino Mountains of southern California.

Although most genecological studies are on wide ranging species, a number of instances of localized variability have been published. Culberson and Culberson (1967) found local ecological sorting of a lichen species on a coastal promontory in North Wales. Briggs (1962) demonstrated a mosaic of local ecotypes of a *Ranunculus* species. Squillace and Bingham (1958) showed localized ecotypic variation in western white pine, related to elevation, slope direction and soil moisture. The work of Kruckeberg (1968) has demonstrated many ecotypes related to narrowly restricted edaphic conditions.

Local ecotypes or ecoclines related to altitude have also been found. Papers from the Carnegie group, typified by Clausen, Keck, and Hiesey (1948) involve altitude as a principal habitat gradient. Other geneco-

typic variation related to altitude has been reported by Britten (1960) in *Trifolium repens*, by Grant and Hunter (1962) in *Calluna vulgaris*, by Mark (1965) in *Chionochloa rigida*, by Pisek and Winkler (1959) in *Picea excelsa*, by Myers and Bormann (1963) in *Abies balsamea*, and, originally, Turesson (1925) in numerous species of herbaceous perennials in Scandinavia.

METHODS

Methods of determining genecological variation have involved various morphological and physiological techniques. In this study a physiological approach was used. Turesson (1925) and Heslop-Harrison (1964) have stressed the importance of the physiological response in genecology. Seedlings were grown from seed collected from several trees at 850 m and 1600 m, the elevational limits of knobcone pine in the study area. They were allowed to develop in the greenhouse in pots of native soil until they possessed a mixture of primary and secondary leaves. This corresponds to two year old seedlings in the field. In June, 1968 the plants were placed in a growth chamber on a 15 hour photoperiod with 13°C days and 5° nights. Previous work (Wright, 1970) had shown 7 days in a temperature regime to promote full acclimation to that regime. Light intensity was 2500 ft-c at plant height, from cool white fluorescent lights. After a minimum of 10 days conditioning each plant was withdrawn and its rate temperature curve of net photosynthesis determined with a CO₂ analyser, as described in an earlier paper (Wright, 1970). Following determination the plants were placed in a regime of 15 hour photoperiod, 32° days, 18° nights. After acclimation to these new conditions the rate temperature curve was again determined for the same plants. There was no leaf loss and little apparent growth during the three weeks between runs on a given plant. Temperature regimes were chosen to represent winter and summer conditions as determined by field studies (Wright, 1966). It was felt that, as Heslop-Harrison (1964) states, experimental variety in environment would bring out the capacity of ecotypes to react to peculiarities which would be masked in a uniform environment. This, Heslop-Harrison pointed out, would be especially true with physiological responses.

RESULTS

Table 1 shows the nature of the rate-temperature curve of photosynthesis when plants have been conditioned to a cold regime and subsequently to a warm regime. Plants from high elevation, when cold-conditioned, were advantaged at high temperatures, 30° and 35°. When warm-conditioned, plants from high elevation were advantaged at all temperatures, but the advantage was greatest at low temperatures. Photosynthetic rate was greater after warm-conditioning than after cold-conditioning with plants from both elevations, but the difference was more marked with high elevation plants. Similar trends were found in *Pinus*

TABLE 1. NET PHOTOSYNTHESIS OF KNOBCONE PINE, MG CO₂/GM LEAF FRESH WT./HR.

	15°	20°	25°	30°	35°
Cold conditioned					
1600 m origin	3.57	2.86	1.95	0.96	-0.19
850 m origin	3.04	2.38	1.64	0.29	-0.83
Warm conditioned					
1600 m origin	6.12	5.41	4.24	3.00	1.73
850 m origin	4.59	3.93	2.86	1.84	0.95

*Significant difference between means

**highly significant difference between means

coulteri D. Don., but sample size was too small to provide conclusive data.

DISCUSSION

The data in Table 1 indicate that in winter when acclimated to cold, the high altitude population would be capable of a higher rate of net photosynthesis during sudden spells of warm weather. In summer when acclimated to heat the high altitude population would have an advantage at all temperatures, but especially during sudden spells of cool weather. The greatest advantage seems to be in conditions that occur infrequently. A lesser but steady advantage obtains for high elevation populations during more normal summer weather. Net photosynthesis in the high altitude population seems to be better buffered against sudden temperature changes. This indicates that response to temperature is critical at upper elevational limits, a thesis supported by most work on upper elevational limits of species (Daubenmire, 1954; Bryson, Irving and Larsen, 1965).

The adaptive value of the genecotypic variation shown by Table 1 is by no means overwhelmingly clear. There may be a case for random genetic drift within small populations (Heslop-Harrison, 1964). Although the distance between elevational extremes is only 5 km, and knobcone pine woodland is continuous, gene exchange over this distance may be slow. Colwell (1951) found that very little of coulter pine pollen released at a height of 12 ft travelled as far as 150 ft, even downwind. The populations of knobcone pines within 150 ft of the collection sites comprise only a handful of trees in each case. Therefore, random non-adaptive genetic drift is a distinct possibility. This indicates that ecotypic variation can be on a very local scale, as indicated by the work of Gregor and Watson (1961), even when no sharp habitat discontinuities occur. Heslop-Harrison (1964) has pointed out that ecotypes will evolve even in the face of crossbreeding if there is a range of habitat conditions, especially if the range is extreme. He suggests that phenological differences, such as time of pollen release, may block free gene flow. This may be the case with these knobcone pines. Kruckeberg (1967) has demonstrated many cases of ecotypes persisting in closely

adjacent sites where preadaptedness for the ultramafic habitat outweighs free gene flow. Bradshaw (1960), working with *Agrostis tenuis* in a small area of central Wales, found changes in genotype to be either gradual or sudden, depending on the smoothness of habitat change. In this study of knobcone pine, apparently selection pressure is high enough to outbalance whatever gene flow occurs, even as judged in seedlings reared artificially where natural selection has not been permitted to operate on the experimental generation. Possibly even more genecotypic variation would be found if experimental plants could be vegetatively propagated from the mature field trees. Future work may employ a grafting technique for rooting fascicle cuttings of pine.

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